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Effects of Combined Frontal and Temporal Lesions on Learned Behaviors in Rhesus Monkeys*

H. F. Harlow,† K. A. Schiltz, A. J. Blomquist, and C. I. Thompson‡

REGIONAL PRIMATE RESEARCH CENTER, UNIVERSITY OF WISCONSIN, MADISON

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Abstract. Delayed response ability, and to a lesser extent visual discrimination performance, is seriously impaired by extensive bilateral damage to the frontal lobes. Reciprocal anatomical connections between the frontal and temporal lobes suggested that massive lesions in both lobes might produce an impairment more complete than that resulting from frontal lobectomy alone. Five monkeys were given combined bilateral frontal and anterior-temporal lesions, and were found to be inferior to both frontal lobectomized monkeys and to unoperated controls on the object discrimination task. The combined lesion did not increase the deficit on delayed response over that obtained after only bilateral frontal lobectomy. Results indicate that the anterior-temporal neocortex is involved in the mediation of visual discrimination ability.

Bilateral destruction of the frontal lobes produces a picture of behavioral deficit which is drastic, but the literature is not entirely precise. Delayed response and single alternation performance are severely impaired,[1] although some sparing of delayed response has been reported when the lesions have been produced at or before 5 months of age,[2] and when older animals have been subjected to intensive training procedures.[3] On the other hand, learning tests of equal or greater difficulty involving visual discriminations show considerable sparing. Large bilateral frontal lesions do produce a performance decrement on object discrimination and object discrimination learning-set tasks, but the loss is not complete.[3,4]

In the hope of achieving more complete and precise behavioral deficits on tasks involving both visual discrimination and delayed response, we examined the combination of bilateral frontal lobectomy with the destruction of other cerebral areas. Kling and Tucker[5] found little or no sparing on the delayed response task after surgery in infant monkeys when they combined frontal lesions with damage to the head of the caudate nucleus. However, this combination did not produce an increased deficit on a red-green discrimination.

Myers[6] pointed out that there is an anatomical rationale for combining destruction of the frontal lobe with bilateral destruction of the anterior portion of the temporal lobes. In general it is known that frontal lobe areas give rise to projections to the temporal lobe and, conversely, the rostral pole of the temporal lobe projects to the frontal lobe. Anatomical studies[7,8] have shown that lesions of frontal cortex superior to the sulcus principalis lead to degeneration of fibers

coursing to the superior temporal lobe, and lesions of frontal cortex inferior to the sulcus principalis produce degenerating fibers in the cortex of the superior temporal sulcus. Lesions of the orbital region of the frontal lobe lead to degeneration of fibers in the temporal pole. In addition, a lesion in the anterior pole of the temporal lobe leads to degeneration of fibers terminating in the orbital and lateral cortex of the frontal lobes. As further emphasis on the relationship between the frontal lobe and anterior temporal lobe, these two cortical regions are considered by some investigators to be parts of a single functional unit.[6]

In the present study no attempt was made to exploit all of these anatomical relationships, but massive bilateral lesions in the frontal lobe were combined with bilateral neocortical lesions in the anterior temporal pole. The effects of this combined lesion upon visual discrimination and delayed response ability were then assessed in comparison with the performance of both normal control subjects and monkeys sustaining damage limited to the frontal lobes.

Method. Subjects: Nineteen rhesus monkeys served as subjects. Four monkeys underwent a bilateral frontal lobectomy at 24 months of age, and hereafter are referred to as Group F. Group C-F (control-frontal) was a like-aged group of four monkeys that served as unoperated controls for Group F. Of the remaining 11 monkeys, five sustained a bilateral frontal lobectomy at 20 months, followed by bilateral removal of the anterior tips of the temporal lobes at 34 months of age. These monkeys are hereafter referred to as the frontal-temporal group (Group FT). Group C-FT consisted of six monkeys that were unoperated, but who otherwise were treated in a manner identical to that of Group FT.

Group F and C-F animals had limited social experience, and had received no learning tests prior to those reported in the present experiment. However, the results of the learning tests described in this paper were included in a report that is now in press.[3] Groups FT and C-FT had received intensive social experience, and also had been introduced to an abbreviated set of learning tests shortly after the frontal lesions were made in Group FT. None of the learning data from Groups FT and C-FT have been published previously. Results of the abbreviated learning tests administered prior to the time the temporal lobes were removed are reported in a paper now in preparation.

Surgery and histology: Frontal operations from Groups F and FT were performed by aspiration in a single stage by means of standard operative techniques that have been described in detail elsewhere.[9,2] Ablations removed the cortex and all underlying fiber systems in Brodmann's areas 9, 10, 11, and 12, but spared the caudate nucleus. A diagram of the lesion is illustrated in Figure 1. Representative histological sections have been published elsewhere. They indicate that all of the lesions were in the planned areas.[2]

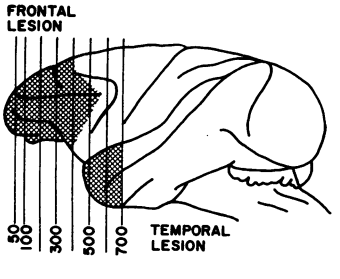

FIG. 1.—Lateral view of rhesus brain. The hatched areas illustrate the location and extent of the frontal lobe and temporal lobe lesion. The numbered lines refer to stained frontal sections from a normal brain used for reconstruction of the lesion in operated animals.

Temporal lesions were made by aspiration in two operations, spaced about 2 weeks apart. All of the temporal neocortex anterior to the inferior aspect of the central sulcus was removed. The area of the lesion is illustrated in Figure 1.

Apparatus. All testing was done in the Wisconsin general test apparatus, which has a superstructure containing a 9 × 24 in. tray with either two or three foodwells, which the observer could cover with stimulus objects and advance within reach of the monkey. Appropriate responses were rewarded by grapes, rai-

sins, small pieces of apple, or shelled corn, depending upon the preferences of individual subjects.

Testing procedure: The adaptation procedure used to accustom monkeys to the test situation has been described elsewhere in detail.[10] The goal of this procedure is to train the monkey to displace stimulus objects of various dimensions in order to uncover a baited foodwell. This goal was accomplished over a period of 7 to 10 weeks for the monkeys in the present study.

After adaptation the monkeys were introduced to a two-object discrimination problem, in which one object ("correct") covered a baited foodwell, and one object ("incorrect") covered an empty foodwell. Each object discrimination problem consisted of presentation of a pair of objects for 25 trials, and a new problem involving a new pair of stimuli was presented each day for 20 days. Each problem was theoretically solvable after a single presentation of the objects, and the dependent measure was the number of correct choices on trials 2–25 for each problem.

Upon completion of object discrimination testing, all subjects were introduced to the delayed-response problem. Stimulus objects consisted of two identical red wooden equilateral triangles 2 in. in depth, which were placed directly over the foodwells. Subjects were allowed to observe a randomly chosen foodwell being baited and, after both foodwells were covered, they were then required to wait either 0 or 5 sec before they were allowed to remove one of the triangles. Ten 0-sec and ten 5-sec trials were given each day for 90 days.

Analyses: Because there were unequal numbers of subjects in the four groups, the data were analyzed by an unweighted means analysis of variance,[11] using a 4×2 (groups $\times$ Problem Blocks) design. Individual group comparisons on object discrimination and delayed response performance were subsequently made, using the Newman-Keuls procedure.[11] The total number of object discrimination problems and delayed response trials was divided into two blocks, and increases in percentage of correct responses with practice were analyzed by the Problem Blocks factor in the analysis of variance.

Results. Object discrimination: As is shown in Figure 2, monkeys subjected to the dual frontal-anterior temporal lesion were inferior to a control group with identical antecedent experience. They also were inferior to the group of monkeys with bilateral frontal lobectomy, and to their control group. The mean number of correct responses out of 480 for the four groups was 402.8 (C-FT), 401.0 (C-F), 388.0 (F), and 345.4 (FT). The standard error of a single mean, used in the Newman-Keuls procedure, is 11.52. Statistically, the two control groups and Group F did not differ, although monkeys with frontal lobectomy showed a tendency to perform at a level somewhat below that of the controls. The performance of Group FT, however, was significantly below that of each of the other three groups (all $ps < 0.05$). Thus it is clear that bilateral removal of the tips of the temporal lobes in monkeys already sustaining frontal lobectomy produces a deficit on object discrimination performance which is greater than that produced by frontal lobectomy alone.

The "Problem Block" factor in the analysis of variance was significant ($p < 0.05$), which indicates that subjects made more correct responses on the second 10 problems than they did on the first 10. Inspection of the data indicated that only two of the 19 subjects, one in Group C-FT and one in Group F, failed to show an improvement on the second block of 10 problems. The Groups $\times$ Problem Blocks interaction was not significant, so there was no evidence that amount of improvement differed among the four groups.

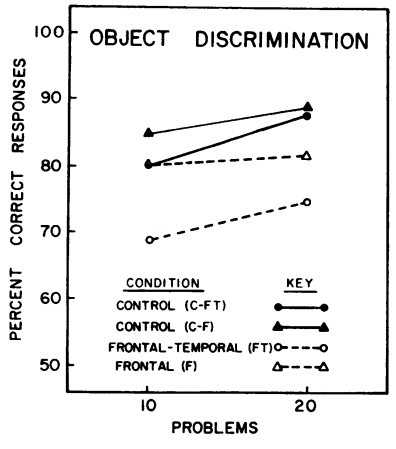

FIG. 2.—Performance of operated groups and normal groups of monkeys on 20 object discrimination problems.

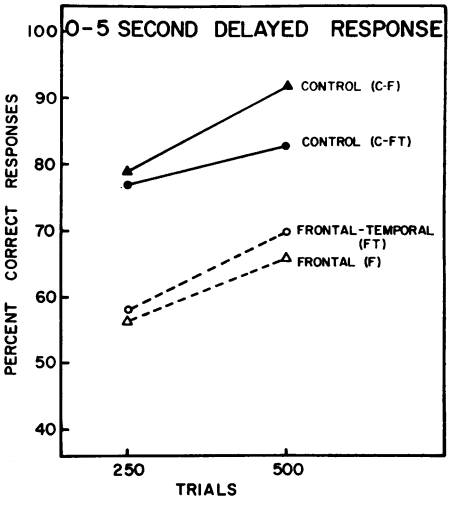

FIG. 3.—Performance of operated and normal monkeys on 500, combined 0-sec and 5-sec, delayed response trials.

0- and 5-second delayed response: As can be seen in Figure 3, the performance on combined 0- and 5-sec delayed response problems of monkeys subjected to bilateral removal of both the anterior temporal and the frontal lobes was drastically impaired, but no more so than was the performance of monkeys subjected to bilateral removal of the frontal lobes alone. The mean number of correct responses on 1000 trials (combining 500 0-sec and 500 5-sec delay trials) for each of the four groups was 854.0 (C-F), 799.2 (C-FT), 641.2 (FT), and 611.2 (F). The standard error of a single mean is 23.35. Statistically, the performance of the frontal-temporal group did not differ from that of the group sustaining only frontal damage. Similarly, the performance of the two control groups did not differ. However, each of the two control groups were superior in performance to Groups F and FT (all four ps <0.01).

The Problem Blocks factor was significant (p <0.01), indicating that subjects made more correct responses on the second 250 trials than they did on the first 250 trials. Inspection of the data revealed that only one of the 19 subjects, in Group C-FT, failed to demonstrate this improvement with practice. The Groups $\times$ Problem Blocks interaction was not significant, so there was no evidence that the four groups differed in their rate of improvement.

Discussion. A wealth of studies has correlated bilateral destruction of functional areas with learned performances. The classical researches by Jacobsen[12] indicated vast delayed response decrement following bilateral destruction of the frontal granular cortex and apparently no loss of other learning capabilities. Since such data were in contradiction to Lashley's[13] theory of equipotentiality of intellectual function, the researches attracted wide attention, apart from their own importance.

Subsequently, it was shown by Pribram[14] and by Harlow and associates[15]

that bilateral frontal lesions and bilateral posterior lesions produced complementary learning syndromes, with discrimination learning and learning-set adversely affected and delayed response unaffected by posterior lesions, and discrimination learning and learning-set almost unimpaired by frontal granular lesions which destroyed or drastically impaired delayed response capabilities. Teuber[16] used the phrase "double dissociation of symptoms" to describe the two differential syndromes.

The double bilateral frontal and anterior-temporal lesion which we described in this paper produced a significant performance decrement on a series of object discrimination problems, when the double-lesioned animals' performance was compared with that of monkeys with bilateral frontal lesions only, or with that of normal controls.

Previously, Meyer,[17] Riopelle *et al.*,[18] and Chow[19] had found that bilateral temporal lobectomy or bilateral temporal decortication impaired discrimination and learning-set performance, but they did not describe the effect of smaller temporal lesions. Pribram[20] has long emphasized that neocortical bilateral temporal lesions adversely affected "visually guided behavior," but he emphasized and reemphasized that the critical temporal-lobe area was the infero-lateral portion of the posterior temporal lobes. The position of the posterior temporal lobes is distinct from the anterior poles, and our data give strong presumptive evidence that the discrimination loss is not limited to lesions in the infero-lateral part of the posterior temporal lobe.

Myers[21] placed a number of monkeys suffering from bilateral destruction of the anterior portions of the temporal lobes in the free environment of an island near Puerto Rico. None of these monkeys rejoined their social groups, and all of them shortly afterwards perished or disappeared. Although we have no measures of the social capabilities of our frontal-temporal monkeys, their extreme intellectual deficits should impose serious hazards to socialization. Thus, there is presumptive evidence that bilateral destruction of the anterior temporal poles impairs social performance as well as learned performance.

The primary finding of the present research was the disclosure that bilateral removal of anterior temporal neocortex superimposed upon bilateral frontal lobectomy significantly impaired performance on a series of 20 object discrimination problems. The lesioned monkeys also showed near total loss of delayed-response performance, but the loss was not greater than that produced by bilateral destruction of the frontal lobes. The results obtained from these combined neocortical lesions suggest that there is reason to believe that multiple lesions of the neocortex made on the basis of anatomical facts will lead to productive research.

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† Requests for reprints may be addressed to Dr. H. F. Harlow, University of Wisconsin, Regional Primate Research Center, 1223 Capitol Court, Madison, Wisc. 53706.

‡ Present address: Department of Behavioral Science, Milton S. Hershey Medical Center, Pennsylvania State University, Hershey, Pa.

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